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Pierre MORET

A contribution to the systematics of Neotropical Platynina. The supra-specific taxa of the *Dyscolus* complex (Coleoptera Carabidae ~~Agonini~~) Platynini

Toulouse

Abstract. The purpose of this paper is to improve the taxonomic treatment of the Neotropical Platynina that have been successively classified as *Colpodes* McLeay and as *Platynus* Bonelli. 14 species, representing 13 existing supra-specific taxa, are analysed cladistically. This analysis is based on 26 morphological characters, 13 of which relate to tarsal structure. Phyletic relationships remain unresolved at three nodes of the proposed cladogram. At the base of the cladogram, *Platynus assimilis* (Paykull) exhibits a more primitive set of characters and therefore can not be congeneric with any South American species. *Glyptolenoides* is the adelphotaxon of *Glyptolenopsis*, whereas the presence of a sulcus on the dorsum of the protibia in *Glyptolenoides* and *Glyptolenus* is considered homoplasic. *Scaphiodactylus* is the adelphotaxon of a clade composed of *Dyscolus* + *Dyscolidion* +[*Stenocnemion* + *Onypteygia*] + *Glyptolenus*.

Резюме. Целью настоящей работы явилось развитие таксономии неотропических Platynina, которые ранее классифицировались как *Colpodes* McLeay и *Platynus* Bonelli. Кладистическому анализу подвергнуто 14 видов, представляющих 13 существующих надвидовых таксонов. Этот анализ основан на 26 морфологических признаках, 13 из которых связаны со структурами лапок. Филетические взаимоотношения остаются нерешенными в трех узлах предложенной кладограммы. В основании кладограммы *Platynus assimilis* (Paykull) демонстрирует более примитивный набор признаков и потому не может относиться к тому же роду, что и любой другой южноамериканский вид. *Glyptolenoides* является сестринским таксоном *Glyptolenopsis*, в то время как присутствие бороздки на дорсальной стороне передних голеней *Glyptolenoides* и *Glyptolenus* считается конвергентным признаком. *Scaphiodactylus* является сестринским таксоном клада, образованного *Dyscolus* + *Dyscolidion* +[*Stenocnemion* + *Onypteygia*] + *Glyptolenus*.

Key words: Coleoptera, Carabidae, Platynini, *Dyscolus* complex, systematics, phylogeny.

INTRODUCTION

During the first half of the 19th century, many species of Neotropical Platynina were described by European entomologists. Some of them were placed in extant genera, namely *Agonum* Bonelli and *Anchomenus* Bonelli, but the greater part were arrayed in eight new genera: *Dyscolus* Dejean, 1831, *Onypterygia* Dejean, 1831, *Stenocnemus* Chaudoir, 1837, *Scaphiodactylus* Chaudoir, 1838, *Paranomus* Chaudoir, 1842, *Ophryodactylus* Chaudoir, 1842, *Pleurosoma* Guérin-Méneville, 1844, *Omiastus* Motschulsky, 1864 and *Metallosomus* Motschulsky, 1864. All these genera, except *Onypterygia*, were subsequently synonymised with *Colpodes* McLeay, 1825, in Maximilien de Chaudoir's two world-wide revisions of the genus *Colpodes* (CHAUDOIR, 1859, 1878). At the same time, the genus *Glyptolenus* was created by BATES (1878) for a group of species presenting a deep sulcus on the dorsal face of the foretibiae. No significant improvements were made during the following century, except for the creation of various ill-defined Mexican supra-specific taxa

by CASEY (1920): *Anacolpodes*, *Hemiplatynus*, *Platynella*, *Stenoplatynus* and *Trapezodera*.

A major shift in the history of the study of American Platynina took place at the beginning of the seventies, when WHITEHEAD (1973), followed later on by LIEBHERR (1986, 1992), transferred all previously described Neotropical *Colpodes* to *Platynus* Bonelli. MORET (1989 a, 1996) and PERRAULT (1990, 1991, 1992) took a different taxonomic option, by giving a new definition to three existing genera (*Dyscolus* Dejean *sensu* MORET, 1989 a; *Scaphiodactylus* Chaudoir *sensu* MORET, 1996; *Stenocnemion* Moret, 1989 a, new name for *Stenocnemus* Chaudoir, nec Mannerheim) and creating four others (*Dyscolidion* Moret, 1990; *Andinocolpodes* Perrault, 1990; *Glyptolenopsis* Perrault, 1991; *Glyptolenoides* Perrault, 1991).

Attempts to reconstruct the phylogeny of Neotropical Platynina have been only partial and not entirely successful. Many characters that are commonly used for distinguishing supra-specific taxa in Carabidae, e.g. the setation of head, pronotum and elytra, prove to be highly inconstant in Platynina. MORET (1989 a) selected characters of the tarsal setation and of the female genitalia that are less subject to variability, but he did not intend to give a complete phylogenetic account of the subtribe. More recently, *Dyscolus memnonius* Dejean and *Stenocnemion acuminatum* (Chevrolat) were included as outgroup taxa in an analysis of the *Platynus degallieri* species group (LIEBHERR, 1992), in order to test the validity of the genera *Dyscolus* and *Stenocnemion*. Unfortunately, the characters that support the diagnosis of these genera, according to MORET (1989 a, 1991), are not taken into account in Liebherr's analysis: neither the number of submental setae, nor the position of apical setae on the apical lobes of the fourth metatarsomere, and not even the duplication of basal elytral setae or the presence of various ventral ensiform setae on the gonocoxites in the case of *Stenocnemion*. Obviously, such a choice induces an a priori bias in the analysis, thus weakening its results as far as the taxa *Dyscolus* and *Stenocnemion* are concerned.

MATERIAL AND METHODS

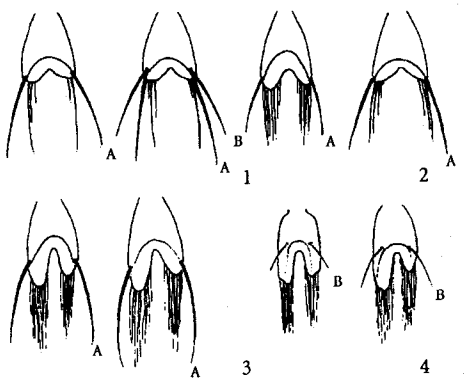
This paper does not attempt a thorough phylogenetic analysis of American Platynina. It is deliberately limited to the analysis of 12 selected species that represent the major known neotropical lineages within the subtribe Platynina (= Platyni sensu LIEBHERR, 1986). My phylogenetic reconstruction therefore depends on previous recognition of monophyletic groups. Monophyly has been assumed for the following taxa, according to complete or partial taxonomic revisions achieved by various authors in the last twenty years : *Agonum* Bonelli, 1809 (LIEBHERR, 1994); *Platynus* Bonelli, 1809, *sensu stricto* (HABU, 1978; MORET, 1989 a; LIEBHERR & WILL, 1996, *pro parte*); *Dyscolus* Dejean, 1831 (MORET, 1989 a, 1996); *Onypterygia* Dejean, 1831 (WHITEHEAD & BALL, 1997); *Dyscolidion* Moret, 1990; *Stenocnemion* Moret, 1989 a (MORET, 1991); *Scaphiodactylus* Chaudoir, 1838 (MORET, 1996); *Glyptolenopsis* Perrault, 1991 (LIEBHERR, 1992); *Glyptolenoides* Perrault, 1991; *Andinocolpodes* Perrault, 1990.

One species was selected in each group to be submitted to a cladistic analysis. The generotypes were generally prefered, unless they present a markedly apotypic set of characters. For example, in *Dyscolus* s. str. the generotype *Dyscolus memnonius* Dejean, from Guadeloupe Island, was replaced by the more plesiotypic and widely distributed *Dyscolus subviolaceus* (Chaudoir, 1842) (= *D. aequinoctialis* Chaudoir, 1850).

Secondly, I took into account two lineages for which monophyly can not be ascertained or is even doubtful. On the one hand, there is a set of North American species currently classified as members of the genus *Platynus* Bonelli (WHITEHEAD, 1973; LIEBHERR & WILL, 1996), though they do not respond to the strict definition of this genus as established by HABU (1978): *P. tenuicollis* (LeConte), *P. brunneomarginatus* (Mannerheim), *P. parmarginatus* Hamilton, *P. ovipennis* (Mannerheim),

P. trifoveolatus Beutenmüller, *P. opaculus* (LeConte), *P. cazieri* Liebherr & Will and *P. cohni* Liebherr & Will, as well as *Platynus (Stenoplatynus) umbripennis* (Casey) and *P. (Hemiplatynus) chihuahuae* Bates. Two of them (*umbripennis* and *chihuahuae*) are analysed herein. On the other hand, the diverse complex of *Glyptolenus* Bates, 1878 (WHITEHEAD, 1974, *pro parte* ; PERRAULT, 1991) is represented by two species showing strong differences in their female genitalia: *G. apicestriatus* (Reiche) and *G. chalybeaus* (Dejean).

Other taxa were discarded for various reasons. *Mexisphodrus* Barr, 1965, *Speocolpodes* Barr, 1974, *Speleodesmoides* Mateu, 1978 and *Tepuydites* Monguzzi & Trezzi, 1993 are highly specialized cavernicolous lineages, most of them known by a single species, and in that species by only one sex. *Incagonum* Liebherr, 1994 is considered exterior to Platynina, in agreement with Liebherr's assumption that this genus belongs to the *Rhadine-Tanystoma* lineage (LIEBHERR, 1994: 6).



Figs 1-4. Fourth mesotarsomere (left) and fourth metatarsomere (right), dorsal view: 1, *Platynus assimilis* (Paykull); 2, *Hemiplatynus chihuahuae* (Bates); 3, *Dyscolus subviolaceus* (Chaudoir); 4, *Glyptolenus apicestriatus* (Reiche). A: latero-apical seta; B: dorsolateral subapical seta. Different scales.

The selected species are all neotropical, except for both type species of *Agonum* and *Platynus*, *Agonum sexpunctatum* (L.) and *Platynus assimilis* (Paykull), which are palearctic. Inclusion of these generotypes in the analysis is intended to give a suitable background for the taxonomic placement of the neotropical lineages.

The phyletic reconstruction which is presented here rejects the principle of parsimony, and therefore does not search for the shortest cladogram. I consider that the principle of parsimony does not reflect the reality of any natural evolutionary process. It is nothing but a conveniance way of selecting one tree among a number of equally possible trees. My cladogram is thus based on a subjective weighing of characters. Subjectivity is expressly assumed, as a consubstantial part of any taxonomic construction.

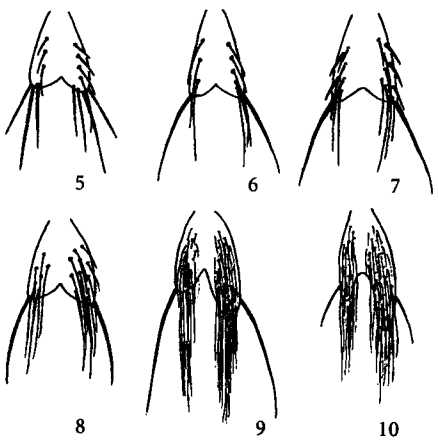
The result is a partly unresolved cladogram (Fig. 20), with eight characters changing twice (1, 3, 6, 7, 10, 11, 12, 25), one character changing three times (22), and one reversal (16).

DISCUSSION OF THE CHARACTER STATES

Most of the characters used in my analysis belong to the morphology of tarsi and female genitalia (Table 1). The reason of this choice is that many other characters that are traditionaly used by carabidologists for segregating supraspecific taxa (shape of the pronotum, number of setae on the surface of head, pronotum and elytra, variations in elytral striae, male aedeagal configuration, etc.), are exceedingly variable in neotropical Platynina, so that no reliable phyletic reconstruction can be supported by them.

Character state polarity was determined using out-group comparison, prior to the construction of the cladogram (Table 2). Polarity assignment is based on previous cladistic analyses by LIEBHERR (1986, 1992) and on personal observations throughout Platyninae. Only the doubtful or debated cases are discussed here.

Characters 1 and 3: constriction of neck and sides of pronotum. In a recent work, Liebherr distinguishes *Agonum* from *Platynus* by the fact that «*Agonum* exhibits a derived condition of more or less orbicular pronotal shape, and *Platynus* possesses the derivation of constricted neck» (LIEBHERR, 1994: 4-5). It is true that



Figs 5-10. Left fourth metatarsomere, ventral view. 5, *Platynus assimilis* (Paykull); 6, *Stenoplatynus umbripennis* Casey; 7, *Hemiplatynus chihuahuae* (Bates); 8, *Scaphiodactylus atratus* (Chaudoir); 9, *Dyscolus subviolaceus* (Chaudoir); 10, *Glyptolenus apicestriatus* (Reiche). Different scales.

most *Agonum* have a rounded pronotum, and that all *Platynus* s. str. (sensu HABU, 1978) possess a dorsally constricted neck. However, these two characters are very variable throughout the Platynina, and in many cases they vary at infrageneric level. Most *Dyscolus* exhibit a constricted neck, but dorsal constriction is absent in many Andean and Mesoamerican brachypterous species of this genus. The shape of the pronotum is an even more variable and unreliable character.

Character 2: setae of submentum. In Platynini, the submentum bears two pairs of lateral setae in the plesiomorphic condition. It has been noted that in *Anchomenus*, *Sericoda* and *Elliptoleus*, this character is quite variable and unreliable for defining generic groups (LIEBHERR, 1991: 13, 123). Yet this variability is peculiar to the *Anchomenus* complex, whereas all other American Platynina exhibit a remarkably stable number of setae. The primitive state of four setae is widely spread among Platynini. The derived state of a single ~~one~~ pair of setae is exhibited by the genera *Platynus* (sensu HABU, 1978) and *Batenus*.

Characters 8 to 18: shape and setation of mid- and hind fourth tarsomeres (Figs 1-10). The relevance of apical setation of the fourth tarsomere was first pointed out by HABU (1978), who made a careful use of it in his systematic revision of Japanese Platyninae. Examination of a great number of American Platynina confirms that the structure of this tarsomere conveys excellent phylogenetic information (in agreement with LIEBHERR, 1992: 94).

- Characters 10, 11, 12: apical configuration of the hind fourth tarsomere. A more or less triangular tarsomere, with a straight or slightly emarginate apex (Fig. 5-8), is primitive (LIEBHERR & ZIMMERMAN, 1998: 155). An elongate tarsomere, with at least a strongly developed outer lobe at apex (Figs 9-10), is considered a derived state.

- Characters 16, 17, 18: apical setae. In the primitive condition, the fourth metatarsomere bears three pairs of apical setae: one dorsolateral, one lateral and one ventrolateral (HABU, 1978; MORET, 1989 a). This character state is exhibited by *Platynus assimilis* (Figs 1, 5) and by various species in *Agonum* (e.g. *A. sexpunctatum*). The rest of *Agonum* and various small lineages (*Synuchus* among Sphodrini, *Anchomenus* and *Sericoda* among Platynini) have lost the outer dorsolateral seta (state not coded here). Both dorsolateral setae are lacking in all known neotropical lineages (with a remarkable exception in *Glyptolenus*, Fig. 4), while the lateral seta has moved to a subapical area (MORET, 1998: 63). In a secondarily derived state, correlated with the lengthening of apical lobes, the loss

Table 1. Description of the primitive (0) and derived (1) states of 26 characters used in the cladistic analysis of Neotropical Platynina.

Character	primitive state (0)	derived state (1)
1. Dorsal surface of neck	constricted accross occiput	not constricted
2. Setae of submentum	2 pairs	1 pair
3. Sides of pronotum	sinuate towards base	rounded or straight towards base
4. Juxtascutellar setation	one seta	no seta
5. Juxtascutellar setation	one seta	two setae
6. Upper face of protibia	convex and smooth	canaliculate or markedly sulcate
7. Upper face of mesotibia	more or less carinulate with various setae in distal part	sharply canaliculate
8. 4th mesotarsomere: ventral setae	one row on each side	unordered setae covering most of the ventral face
9. 4th mesotarsomere: lateral / dorsolateral setae (on each lobe)	apical lateral seta present, dorsolateral subapical seta absent	dorsolateral subapical seta present, apical lateral seta absent
10. 4th metatarsomere: general shape	broadened after middle, with divergent sides	elongate with parallel apical lobes
11. 4th metatarsomere: asymmetry of lobes	outer lobe slightly longer than inner lobe	outer lobe at least 1,5 x longer than inner lobe
12. 4th metatarsomere: outer lobe	ventral excrescence of the lobe reduced, not protruding beyond dorsal apex	ventral excrescence of the lobe protruding beyond dorsal apex
13. 4th metatarsomere: form of ventral setae	normal	dimorphic: bristle-like along margin, thin at middle
14. 4th metatarsomere: disposition of ventral setae	one row on each side	two rows on outer side, one or two rows on inner side
15. 4th metatarsomere: disposition of ventral setae	one row on each side	unordered setae covering most of the ventral face
16. 4th metatarsomere: subapical dorsolateral seta	present on both sides	absent on both sides
17. 4th metatarsomere: latero-apical seta	present on both sides	absent on outer side
18. 4th metatarsomere: latero-apical seta	present on both sides	absent on both sides
19. 5th tarsomere (all legs)	1 pair of dorso-lateral setae near apex	2 pairs of dorsal setae near apex
20. Claws of 5th tarsomeres	smooth	chelate, with long pectinations
21. Apical gonocoxite: ensiform setae	restricted to external margin, none ventral	moved to ventral face, often numerous
22. Bursa copulatrix: microtrichial vestiture	absent or minute, visible only at high magnification	median ring-shaped area of dense microtrichia
23. Dorsum of bursa copulatrix, median lobe	absent or, if present, much narrower than bursa	lobe as broad or broader than bursa
24. Base of bursa copulatrix	without asymetric lobe	with a big lobe on the right side
25. Spermathecal duct	shorter to slightly longer than spermatheca	more than 3 times longer than spermatheca
26. Spermatheca	simple	bipartite apical reservoir

of the lateral seta is observed on one lobe (*Dyscolidion*) or on both lobes (*Tepuydites*).

- Characters 8, 14, 15: setation of the ventral surface. Three states are observed in this set of species. In the primitive condition, two parallel rows of setae are separated by a bare space (Figs 5-6). In a second state, represented here by *Hemiplatynus chihuahuae* (Bates), there is a double row of setae on each side (Fig. 7). In a third state, two brushes of unordered setae cover the major part of the ventral surface (Figs 8-10).

Though the brush-like vestiture is most probably a derived state, there is no reason for assuming that this increase in ventral tarsal vestiture is an adaptation to locomotion on arboreal surfaces (LIEBHERR, 1992: 96; LIEBHERR & ZIMMERMAN, 1998: 154). According to my field observations in South America, many species of the *Dyscolus* complex exhibit brush-like vestitures beneath their tarsi, though they are strictly humicolous or ripicolous, not arboricolous. On the contrary, various arboricolous species of the genus *Glyptolenoides*, found on epiphytes in the montane cloud forest of Ecuador, exhibit the primitive two-rowed state of the character.

Characters 21 to 26: female genitalia (Figs 11-19).Genitalic differences are weak in the subtribe Platynina. Three derived character states (23, 24, 26) are restricted to a single taxon, thus useless for reconstructing phyletic relationships among the subtribe. No genitalic character states were found that could serve to support suprageneric groupings, except for character 21 (setation of apical gonocoxite) that unites *Stenocnemion* and *Onypterygia*.

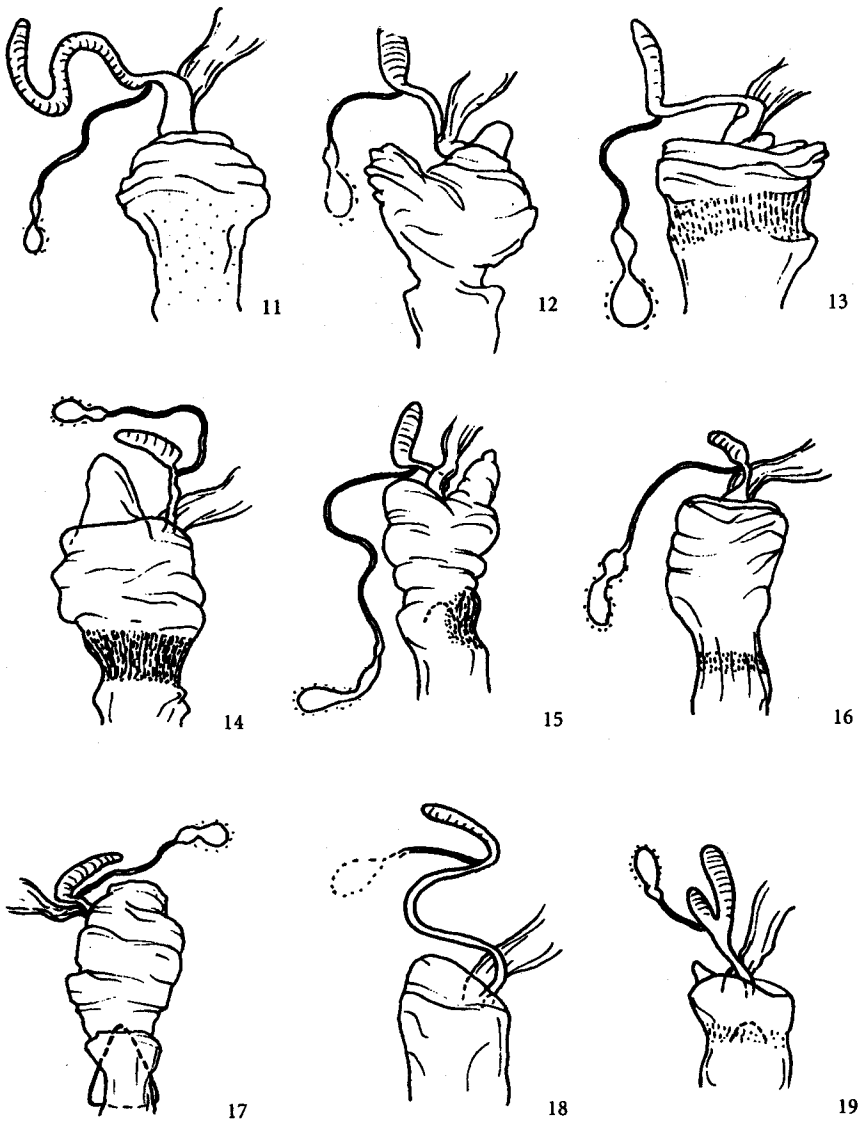
TAXONOMIC RESULTS

The use of the taxon *Platynus* in a broad sense, embracing *Colpodes*, *Batenus*, *Glyptolenopsis*, *Stenocnemion* and *Dyscolus*, as stated first by WHITEHEAD (1973) and more recently by LIEBHERR (1986, 1992), is not supported by the reconstructed phylogeny that I propose here (Fig. 20). The basal trichotomy of the cladogram leads to the separation of three supra-generic groups.

- The *Platynus* complex includes *Platynus* and a little number of allied holarctic genera. *Platynus assimilis* is the most primitive species of our set. It codes only for the condition of reduced setation of submentum, a derived state which is shared by all the species of this holarctic genus, as defined by HABU (1978). The tarsal conditions of *Platynus* are remarkably plesiomorphic (Figs 1, 5). Liebherr's cladogram too, although constructed with a largely different set of characters, gives to *Platynus assimilis* an isolated position, basal to all Platynina (LIEBHERR, 1992: 95).

- The *Agonum* complex, defined as mostly holarctic and Laurasian by LIEBHERR (1994: 2), is not represented in the tropical New World. A few Andean species, erroneously identified as *Agonum* (MORET, 1989 b), must be assigned to the genus *Incagonum* Liebherr, 1994, which belongs to the *Rhadine-Tanystoma* lineage.

- The *Dyscolus* complex, subject of this work, includes *Dyscolus*, *Glyptolenus*, *Onypterygia* and other related taxa. It is defined by the loss of the subapical dorsolateral seta on both sides of the fourth metatarsomere (character 16, figs 2-3). All the members of this complex, except *Stenoplatynus*, exhibit a brush-like vestiture on ventral face of the fourth mesotarsomere (character 8, figs 2-4). Only



Figs 11-19. Bursa copulatrix and spermatheca, ventral view: 11, *Platynus assimilis* (Paykull); 12, *Scaphiodactylus atratus* (Chaudoir); 13, *Andinocolpodes monasterioi* Perrault; 14, *Dyscolus megacephalus* (Bates); 15, *Stenocnemion cycloderum* (Chaudoir); 16, *Onypterygia tricolor* Dejean; 17, *Dyscolidion cyanellum* (Chaudoir); 18, *Glyptolenus apicestriatus* (Reiche); 19, *Glyptolenus chalybaeus* (Dejean), adapted from LIEBHERR, 1988. Different scales.

the terminal clades (*Scaphiodactylus*, *Dyscolus*, *Dyscolidion*, *Stenocnemion*, *Onypterygia*, *Glyptolenus*) possess a brush-like vestiture beneath the fourth metatarsomere as well (character 15, figs 8-10).

Relationships among the clades of the *Dyscolus* complex were not fully resolved. *Andinocolpodes* and *Hemiplatynus* could have been placed in the same

clade owing to the shared derived character of a ring-shaped area of microtrichia on bursa copulatrix (Fig. 13), but the overall differences are so big that I prefer to treat this condition as homoplasic.

Glyptolenoides is the adelphotaxon of *Glyptolenopsis*, whereas the presence of a sulcus on dorsum of protibia in *Glyptolenoides* and *Glyptolenus* is considered homoplasic.

Scaphiodactylus is the adelphotaxon of a clade composed of *Dyscolus* + *Dyscolidion* +[*Stenocnemion* + *Onypteygia*] + *Glyptolenus*, but phyletic relationships between these taxa remain unclear.

Hemiplatynus and *Stenoplatynus* (originally described by Casey as a subgenus of *Hemiplatynus*) probably are valid genera, considering their isolated positions in the cladogram. Nevertheless, any taxonomic decision would be premature as long as an overall revision of the Mexican lineages of Platynina is not achieved.

Although not fully resolved, this cladogram supports the recognition of the following taxa as valid genera:

1. *Andinocolpodes* Perrault, 1990

A very specialized high-altitude lineage, restricted to the Andes of Merida in Venezuela (three brachypterous species). Characterization of *Andinocolpodes* rests on two apomorphic traits: juxtascutellar seta lacking, and onychium with two pairs of dorsal setae near apex.

2. *Glyptolenopsis* (Perrault, 1991) Liebherr, 1992

DIAGNOSIS. Body size small; dorsal surface of neck not constricted; upper face of mesotibia sharply canaliculate (but superior face of protibia is convex and smooth); ventral surface of the fourth metatarsomere with two rows of setae.

This genus includes thirty-six Mexican and Middle American species, two of which are also present in northern tropical South America.

3. *Glyptolenoides* Perrault, 1991

DIAGNOSIS. Dorsal surface of neck constricted; upper face of protibia and mesotibia canaliculate; ventral surface of the fourth metatarsomere with two rows of setae.

Eight species (plus at least three undescribed species) in montane forests of the Andean area, from Venezuela to Bolivia, and one species in Mexico.

4. *Scaphiodactylus* (Chaudoir, 1838), n. stat.

Dyscolus (Scaphiodactylus), Moret, 1996. Type species : *Feronia moesta* Dejean, 1831 (designated by MORET, 1996: 496).

The genus *Scaphiodactylus* is here restricted to the species exhibiting the following set of characters: apical lobes of the fourth metatarsomere slightly asymmetric, the ventral excrescence of the outer lobe not protruding beyond dorsal apex (Fig. 8); ventral surface of the fourth metatarsomere with unordered vestiture of brush-like setae (Fig. 8); microtrichia of the bursa copulatrix scarce and minute, not ring-shaped (Fig. 12).

Part of the species listed as *Scaphiodactylus* by MORET (1996: 498) do not fit with this new diagnosis and must be placed in *Dyscolus*, for example *D. cyanodorsalis* (Liebherr) and *D. robustus* (Chaudoir). *Scaphiodactylus* includes a moderate number of mesoamerican species, one of them spread south along the Andean Cordillera [*S. atratus* (Chaudoir)].

5. *Dyscolus* (Dejean, 1831) Moret, 1989 a

DIAGNOSIS. Outer lobe of the fourth metatarsomere at least 1.5 times longer than

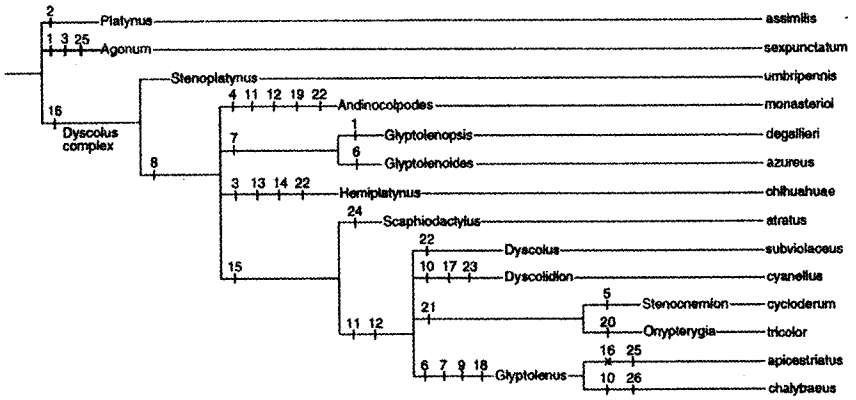


Fig. 20. Preferred cladogram for *Platynus*, *Agonum* and 12 selected taxa of Neotropical Platynina. Hash marks indicate character state advances, x indicates reversal. Character numbers correspond to table 1.

inner lobe, its ventral excrescence protruding beyond dorsal apex (Fig. 3); unordered setae covering most of the ventral face of the fourth metatarsomere (Fig. 9); bursa copulatrix with a median ring-shaped area of dense microtrichia (Fig. 14) (for the latter, reversal to primitive condition is exhibited by a few brachypterous species).

This highly diverse genus is represented by hundreds of species in all tropical America, from North Argentina to Mexico and the Caribbean Islands. 159 species have been already described in South America, but this number amounts for only a third of the species I have seen in various European and American collections.

6. *Dyscolidion* Moret, 1990

DIAGNOSIS. Elytral striae punctate; surface of elytra shiny, with metallic luster; outer lobe of the fourth metatarsomere longer than basal part of the segment; unordered setae covering most of the ventral face of the fourth metatarsomere; latero-apical seta present on inner lobe, lacking on outer lobe of the fourth metatarsomere; bursa copulatrix glabrous, with a broad triangular lobe on dorsum (Fig. 17).

Twenty-six species in tropical Mexico and Middle America, seventeen species in tropical South America, mostly in the Andes. I have seen eighteen more undescribed species from South America.

7. *Stenocnemion* (Moret, 1989 a) Moret, 1991

DIAGNOSIS. Body shape slender; two juxtascutellar setae on each elytron; fourth metatarsomere bilobed, with unordered setae covering most of the ventral face; apical female gonocoxite with ensiform setae on ventral face.

Ten species in Mexico and Middle America, one species in Western Ecuador.

8. *Onypterygia* (Dejean, 1831) Whitehead & Ball, 1997

DIAGNOSIS. Claws of the fifth tarsomeres chelate, with long pectinations; apical female gonocoxite with ensiform setae on ventral face.

Thirty-four species in Mexico and Middle America.

9. *Glyptolenus* (Bates, 1878) Perrault, 1991

DIAGNOSIS. Superior face of protibia and mesotibia canaliculate; dorsolateral subapical setae present on fourth mesotarsomere; latero-apical setae lacking on fourth mesotarsomere and metatarsomere (Fig. 4); fourth metatarsomere bilobed, with unordered setae covering most of the ventral face (Fig. 10).

Fourteen described species, and more than twenty undescribed species in Mesoamerica and tropical South America.

Key to the South American epigeous genera of the *Dyscolus* complex (external characters)

1. Onychium with one pair of dorsal setae near apex 2
- Onychium with two pairs of dorsal setae near apex. . . . . .*Andinocolpodes*

2 (1). Ventral face of the 4th metatarsomere with two rows of setae. 3
- Ventral face of the 4th metatarsomere with a brush-like unordered setation. 4

3 (2). Upper face of protibia convex and smooth; neck not constricted dorsally. . . . . *Glyptolenopsis*
- Upper face of protibia canaliculate or carinulate; neck constricted dorsally .. . . . . *Glyptolenoides*

4 (2). Apical lobes of the 4th metatarsomere slightly asymmetric, the ventral excrescence of the outer lobe not protruding beyond dorsal apex. . . . . *Scaphiodactylus*
- Outer lobe of the 4th metatarsomere at least 1,5 times longer than inner lobe, its ventral excrescence protruding beyond dorsal apex. 5

5 (4). Latero-apical seta present on both lobes of 4th metatarsomere. 6
- Latero-apical seta lacking at least on outer lobe of 4th metatarsomere. 7

6 (5). Two juxtascutellar setae on each elytron; 4th metatarsomere with lateral setae inserted on dorsal apex of lobes. . . . . *Stenocnemion*
- One juxtascutellar seta on each elytron (except *D. antoninus* Moret); 4th metatarsomere with lateral setae inserted subapically. . . . . .*Dyscolus*

7 (5). Upper face of protibia canaliculate; latero-apical setae lacking on both lobes of 4th metatarsomere . . . . . .*Glyptolenus*
- Upper face of protibia convex and smooth; latero-apical seta present on inner lobe, lacking on outer lobe of 4th metatarsomere. . . . . *Dyscolidion*

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Table 2. Character-state matrix for *Platynus*, *Agonum* and 12 selected taxa of Neotropical Platynina: 0, primitive state; 1, derived state; x indicates that the character state changes in other species of the same genus.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
"A. 6-punctatum"	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
"P. assimilis"	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
"St. umbripennis"	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
"H. chihuahuae"	0	0	1	0	0	0	0	1	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0
"A. monasterioi"	x	0	0	1	0	0	0	1	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0
"G. degallieri"	1	0	x	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	x	0	0	0	0
"G. azureus"	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
"Sc. atratus"	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0
"D. subviolaceus"	x	0	x	0	0	0	0	1	0	0	1	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0
"D. cyanellus"	0	0	x	0	0	0	0	1	0	1	1	1	0	0	1	1	1	0	0	0	0	0	1	0	0	0
"St. cycloderum"	0	0	x	0	1	0	0	1	0	0	x	x	0	0	1	1	0	0	0	0	1	x	0	0	0	0
"0. tricolor"	0	0	x	0	0	0	0	1	0	0	1	1	0	0	1	1	0	0	0	1	1	x	0	0	0	0
"G. apicestriatus"	0	0	0	0	0	1	1	1	1	0	1	1	0	0	1	0	0	1	0	0	0	0	0	0	1	0
"B. chalybaeus"	0	0	0	0	0	1	1	1	1	1	1	1	0	0	1	1	0	1	0	0	0	0	0	0	0	1

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Author's address:
P. Moret, 13 rue Léo Delibes, F - 31200 Toulouse (France). E-mail: moret@univ-tlse2.fr